THE ORIGIN OF CORN

V. A Critique of Current Theories

BY

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In the previous papers in this series (22, 23, 24, 32), we have reviewed the objections to and the evidence supporting our tripartite theory on the origin and evolution of corn. We have shown that the factual evidence for some parts of this theory has increased substantially during the last two decades, and that nothing has yet come to our attention which completely rules out any part of it.

The hypothesis that the original corn was a type of pod corn is all but proven by archaeological evidence and by a genetic reconstruction of the ancestral form (15, 16, 17, 19, 20). Because of the discovery of fossil corn pollen in Mexico, the view that corn originated in South America is less satisfactory now than it was twenty years ago, but the hypothesis of a South American origin is not yet completely untenable since research on some phases of this problem, such as that on fossil pollen, has only begun.

The evidence that teosinte (*Zea mexicana*) originated as a hybrid between corn and Tripsacum is decidedly stronger now than when the hypothesis was first presented and, contrary to opinions of several other workers, there is no sound evidence against the hypothesis. We have always recognized that this part of the tripartite theory cannot easily be tested. We have never consid-

ered the probability to be great that a "good" teosinte could be synthesized by hybridizing corn and Tripsacum in experimental cultures, and we have given reasons for this.

The recent evidence is decidedly in favor of the view that introgression between corn and teosinte has been frequent and that it has been effective in producing innumerable new varieties and forms, both ancient and modern. We now consider that this third part of the tripartite theory is almost an established fact.

It should be clear from the contents of previous papers in this series that we consider the tripartite theory to be better supported by factual evidence than any other explanation of the origin of corn proposed up to the present. The fact that we are still committed to the tripartite theory, however, should not prevent us from considering alternative theories and this we shall attempt to do objectively, if briefly, in this final paper.

The Papyrescent (*Semivestidos*) Theory

This is no more than a slight modification of the pod-corn theory. Andres (1) discovered in Argentine maize a type which superficially resembles a weak form of pod corn. Apparently unaware that Bonvicini (5) in Italy had described this character many years earlier and had given it the name "palee sviluppate," Andres called the type "semivestidos" and suggested that it, rather than pod corn, might be the ancestral form.

The character has recently been given still a third and probably more appropriate name "papyrescent" by Galinat (10), whose studies show that the glumes of this type become soft and papery as they mature. Unlike pod corn, which although sometimes monstrous still represents a combination of normal characteristics found in other grasses, papyrescent is a defect in development which it

is difficult to regard as constituting the primitive form of modern corn. No archaeological specimens of papyrescent corn have been reported.

As was pointed out in the first paper in this series, Weatherwax (41), in discussing one aspect of the pod-corn theory, apparently confused papyrescent maize and a weak form of pod corn, half-tunicate. His illustration (Fig. 51) of half-tunicate maize is almost certainly a photograph of papyrescent maize.

The Corn Grass Theory

Singleton (35) has suggested that the ancestral form of modern corn is "corn grass." This anomalous type, the product of a single dominant gene, produces numerous tillers and small "ears" with a high proportion of single spikelets. Many of the kernels are partly enclosed in bracts, but the majority of these are not glumes but spathes.

He also suggested that, if a plant of corn grass were found in nature, it would not be recognized as maize and would almost certainly be regarded as a different species if not a different genus. This may be true, and it illustrates how the maize plant can be drastically changed by a single gene mutation. If corn grass were the ancestral form, a mutation at a single locus could have transformed it from a wild, almost useless, plant to the unique cereal which maize is today.

Although corn grass has some of the characteristics which we might expect to find in an ancestral form — for example, a freely-tillering habit — it lacks others, such as the regular development of prominent glumes. At the other extreme, it has characters which are not demanded of a hypothetical ancestor. One of these, single spikelets (9), represents a condition more specialized instead of more primitive than the paired spikelets of mod-

ern maize. Another, a well-developed spathe, suggests the ancestral form not of maize but of *Coix*, whose fruit case has been found by Weatherwax (39) to comprise a spathe and a segment of the rachis. Corn grass probably is, as Galinat (8) has suggested, a "false" progenitor of maize, exhibiting certain traits which might have occurred in a remote ancestor of the *Maydeae*.

Finally, the evidence from archaeological maize does not support the corn grass theory. Prehistoric maize had prominent glumes, but it did not have the long spathes of corn grass. The possibility that corn grass is the ancestral form appears to us to be remote indeed.

The Teosinte Theory

The theory that maize originated as a domesticated form of teosinte—its nearest known relative—was first proposed by Ascherson (2). Later students, notably Harshberger (12) and Collins (6), modified the theory postulating that one parent of corn is teosinte and the other is a grass now unknown. As teosinte occurs naturally only in Mexico and Central America, supporters of this theory have usually assumed that both teosinte and maize originated in that region. We (21) concluded that teosinte is the progeny rather than the progenitor of maize — the product of the natural hybridization of maize and its wild relative, Tripsacum. Teosinte, however, plays an important role in the tripartite theory, for this theory holds that the many modern varieties of maize are the product of the introgression of teosinte into maize.

Since 1939, new evidence has been presented both in support of and in contradiction to the teosinte theory.

Beadle's (4) discovery that the seeds of teosinte will "pop" when exposed to heat, shattering the hard, bony shell in which they are enclosed, shows one way in which teosinte might have been used as a food plant and weak-

ens the objection that a species so unpromising for food purposes would never have been domesticated. There is no evidence, however, archaeological, historical or contemporary, to show that teosinte was ever employed for food in this manner. When teosinte is used for food, as it occasionally is today in times of food shortage, the fruits are crushed on a metate or with a mortar and pestle, and the meal of the crushed caryopses is separated from the fragments of the bony fruit case.[1]

Langham's (13) data on the inheritance of characteristics which distinguish teosinte and maize indicate simple Mendelian inheritance for several characters and lend some support to Emerson's (unpublished) contention that a few large scale mutations could transform teosinte into maize. But the much more extensive data of Mangelsdorf (14) and of Rogers (33, 34) show that the genes which distinguish maize and teosinte are numerous and are distributed among a majority of the chromosomes. The highly significant studies of Rogers seem to have been completley overlooked by both Weatherwax and Randolph; at least they are not cited in their extensive bibliographies.

The recent studies of Barghoorn, Wolfe and Clisby (3) on fossil pollen in Mexico lend no support to the teosinte theory. Although pollen of both maize and Tripsacum was found at great depths, the pollen of teosinte occurred only near the surface in the upper levels of the drill core where maize pollen was abundant suggesting that the practice of agriculture had begun. Furthermore, the maize pollen found at the lower levels is as large as any modern maize pollen and shows no resemblance to teosinte pollen in the ratio of total diameter to the diameter of its pore. If this fossil pollen is as old as it is estimated to be — 80,000 years or more — the

[1] Personal communication from the late R. H. Barlow.

theory that maize originated from teosinte under domestication can now be safely ruled out.

Recent studies of archaeological maize, like those of fossil pollen, do not support the teosinte theory. On the contrary, they show that the earliest maize was less like teosinte, whereas some recent maize is more like it. Archaeological specimens exhibiting characteristics of teosinte, including distichous ears, single spikelets and highly lignified rachises and glumes, have been found in several sites. But these are always recent specimens and are interpreted as being products of the introgression of teosinte into cultivated maize (7, 11, 19, 20, 25).

A series of studies on the morphology of the corn ear has a bearing on the teosinte theory, because many workers who favored this theory explained the polystichous character of the corn ear as the result of the lateral fusion of several teosinte spikes. The voluminous literature on this subject was reviewed by Mangelsdorf and Reeves in 1939 (21) and more recently by Nickerson (27). The present status of the problem is that evidence for the lateral fusion of two-rowed spikes to form the polystichous ear is completely lacking; the only evidence found for fusion is the adnation of the rachis flaps (prophylls) to the main axis of the cob. It may be concluded, therefore, that the structure of the corn ear has thus far shown no evidence that corn is a descendant of teosinte.

The Theory of Common Ancestry

It appears that Montgomery (26) was the first to propose the theory of common ancestry, although he did not include Tripsacum in the alliance with corn and teosinte. Weatherwax (37) formulated the theory as we now know it, by adding Tripsacum to the two species considered by Montgomery, and he defended it in subsequent publications (38, 40, 41, 42). Randolph (28, 29)

agreed with Weatherwax, with reservations; he still regards the direct descent of corn from teosinte as a distinct possibility.

The theory of common ancestry maintains that corn originated from a perennial, wild, corn-like ancestor, now extinct, and that this extinct ancestor, sometimes called pre-maize, in turn had an ancestor, likewise extinct, in common with teosinte and Tripsacum; also that the native range of all of these species was Central America and Mexico. Actually the theory represents the application to the American *Maydeae* of the broad views of Darwin and earlier students of evolution.

The factual evidence claimed by the proponents of this theory falls into two categories. (A) The three groups—corn, teosinte and Tripsacum—are very similar, except that each has modifications of its own which have led to the differences now found among them. For example, teosinte and Tripsacum have lost one member of each original pair of pistillate spikelets, but corn has not; most varieties of corn and teosinte have lost the terminal staminate portion of the lateral inflorescence (ear), but Tripsacum has not. Weatherwax (41, 42) pointed out by way of explanation that, if we could restore to each of the three groups the primitive organs which have been modified in evolution, they would converge in a common type, giving us an idea of the common ancestor. But more revealing, in our opinion, is the result that would be obtained by restoring the primitive organs of only corn and Tripsacum, omitting teosinte. The common type towards which they would converge is the same as when teosinte is included. This fact is best explained by the hypothesis of the hybrid origin of teosinte, because this hypothesis holds that the characters of teosinte are merely a combination of those of corn and Tripsacum.

(B) It is stated that corn, teosinte and Tripsacum are

now sympatric only in Central America and Mexico, and for this reason all of them probably originated from a common ancestor which also occurred there. When the fallacy of placing such strong reliance on this present-day distribution is recognized, little or no factual evidence for the theory of common ancestry remains. Stebbins (36) reviews the literature on the theory that centers of diversity correspond to centers of origin. He points out that the theory has many pitfalls, except when the group in question is young and the selective forces of the environment have been operating in about the same manner throughout its evolutionary history. Stebbins shows that related genera, congeneric species and even conspecific populations might be expected to have widely disjunct ranges. He cites numerous examples of a single species with two ranges separated by half the distance around the earth. He shows also that examples of closely related disjunct taxa are not rare exceptions but are numerous and that some of them have been known since the time of Darwin.

Much of the validity of the Montgomery-Weatherwax theory depends upon the assumed correlation between the common ancestry and the common place of origin of the three groups. If one or two of the groups were shown to have originated elsewhere than in the present center of diversity (and this may yet prove to be true especially of Tripsacum), this would seriously weaken the theory. In addition, the proponents of the theory assume the previous existence of a pre-maize and of the common ancestor of pre-maize, teosinte and Tripsacum without one iota of evidence. The tripartite theory, in contrast, is more flexible and much less dependent upon completely unknown ancestors of corn. Indeed, it requires no ancestral types other than forms still in existence. Types of pod corn very similar to our hypothetical an-

cestor occur today; types of Tripsacum and corn which come extremely near to satisfying the requirements for the putative parents of teosinte are well known. Yet Weatherwax (41,42) states that it is the tripartite theory, rather than the "simple" theory of common ancestry, which "is topheavy with assumptions of such character that if one of them should be rejected the whole structure would fall."

The theory of common ancestry has two additional weaknesses which are serious: (A) It does not, Weatherwax's and Randolph's contentions to the contrary, notwithstanding, explain all of the known facts. (B) It can not easily be tested.

A. Some of the facts which the theory of common ancestry does not explain are discussed in detail in other papers of this series (23, 32). Here it will suffice to point out that the theory does not account for the facts that (a) teosinte is intermediate between maize and Tripsacum in a great majority of its characteristics (21, 31); (b) early archaeological maize is more "maize-like" than later maize (7, 11, 19, 20, 25); (c) fossil pollen of maize and Tripsacum were found at great depths at one site in Mexico, whereas teosinte pollen occurred only in the upper levels of the drill core; (d) forms of pod corn are now in existence which possess all of the characteristics expected in the ancestral form (16, 17); (e) variation in knob numbers is correlated with tripsacoid characteristics (18), and with proximity to Guatemala, the reputed center of origin of teosinte (21, 30).

B. The theory is largely untestable, because the only evidence which could prove it to be correct beyond a reasonable doubt would be the discovery of prehistoric remains, antedating agriculture, of all three groups of the American *Maydeae* and of the remote ancestor from which these three groups stem. Since it is largely untest-

able, it neither stimulates new research nor points to possible new methods of maize improvement. In this respect, the theory is less useful than the tripartite theory which has furnished the impetus for an extensive series of researches on maize and its relatives and has also suggested new possibilities for improving maize. If two theories appear to be equal in validity, the one which is testable and which stimulates new research is the more useful; a theory which is plausible but untestable tends to stifle research.

In emphasizing the differences between the tripartite theory and that of common ancestry it should not be overlooked that there are also important resemblances between them. The two theories agree that (a) corn is an American plant; (b) it is descended, with Tripsacum, from a remote common ancestor; (c) its immediate ancestor was a freely-branching plant bearing small ears with grains enclosed in glumes; (d) corn attained its present form through changes occurring during domestication, which began not more than a few thousand years ago. In a broad sense, then, the two theories agree with respect to the place, time and manner of origin. In the same broad sense, the problem of the origin of corn can almost be said to be solved.

LITERATURE CITED

1. Andres, J. M., 1950. Granos semivestidos, restos de un carácter ancestral del maiz. Revista Argentina de Agron. 17: 252–256.

2. Ascherson, P., 1875. Ueber *Euchlaena mexicana* Schrad. Bot. Vereins Prov. Brandenburg 17: 76–80.

3. Barghoorn, E. S., M. K. Wolfe and K. H. Clisby, 1954. Fossil remains from the Valley of Mexico. Bot. Mus. Leafl. Harvard Univ. 16: 229–240.

4. Beadle, G. W., 1939. Teosinte and the origin of maize. Jour. Hered. 30: 245–247.

5. Bonvicini, M., 1932. Sulla eraditarietà di una anomalia nel mais. L'Italia Agricola 69: 3–9.

6. Collins, G. N., 1912. Origin of maize. Jour. Washington Acad. Sci. 2: 520–530.

7. Cutler, H. C., 1952. A preliminary survey of plant remains of Tularosa Cave. Fieldiana: Anthropology (Chicago Nat. Hist. Mus.) 40: 461–479.

8. Galinat, W. C., 1954. Corn grass I. Corn grass as a possible prototype or a false progenitor of maize. Amer. Nat. 88: 101–104.

9. ——, 1954. Corn grass II. Effect of the corn grass gene on the development of the maize inflorescence. Amer. Jour. Bot. 41: 803–806.

10. ——, 1957. The effects of certain genes on the outer pistillate glume of maize. Bot. Mus. Leafl. Harvard Univ. 18: 57–76.

11. ——, P. C. Mangelsdorf and L. Pierson, 1956. Estimates of teosinte introgression in archaeological maize. Bot. Mus. Leafl. Harvard Univ. 17: 101–124.

12. Harshberger, J. W., 1896. Fertile crosses of teosinte and maize. Gard. and Forest 9: 522–523.

13. Langham, D. G., 1940. The inheritance of intergeneric differences in Zea-Euchlaena hybrids. Genetics 25: 88–107.

14. Mangelsdorf, P. C., 1947. The origin and evolution of maize. Advances in Genetics 1: 161–207.

15. ——, 1948. The role of pod corn in the origin and evolution of maize. Ann. Missouri Bot. Gard. 35: 377–406.

16. ——, 1958. Reconstructing the ancestor of corn. Proc. Amer. Philos. Soc. 102: 454–463.

17. ——, 1958. Ancestor of corn. Science 128: 1313–1320.

18. —— and J. W. Cameron, 1942. Western Guatemala, a secondary center of origin of cultivated maize varieties. Bot. Mus. Leafl. Harvard Univ. 10: 217–252.

19. —— and R. H. Lister, 1956. Archaeological evidence on the evolution of maize in northwestern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 151–178.

20. ——, R. S. MacNeish and W. C. Galinat, 1956. Archaeological evidence on the diffusion and evolution of maize in northeastern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 125–150.

21. —— and R. G. Reeves, 1939. The origin of Indian corn and its relatives. Texas Agric. Exp. Sta. Bull. 574: 1–315.

22. —— and R. G. Reeves, 1959. The origin of corn. I. Pod corn, the ancestral form. Bot. Mus. Leafl. Harvard Univ. 18: 329–356.

23. —— and R. G. Reeves, 1959. The origin of corn. III. Modern races, the product of teosinte introgression. Bot. Mus. Leafl. Harvard Univ. 18: 389–411.

24. —— and R. G. Reeves, 1959. The origin of corn. IV. Place and time of origin. Bot. Mus. Leafl. Harvard Univ. 18: 413–427.

25. —— and C. E. Smith, Jr., 1949. New archaeological evidence on evolution in maize. Bot. Mus. Leafl. Harvard Univ. 13: 213–247.

26. Montgomery, E. G., 1906. What is an ear of corn? Pop. Sci. Month. 68: 55–62.

27. Nickerson, N. H., 1954. Morphological analysis of the maize ear. Amer. Jour. Bot. 41: 87–92.

28. Randolph, L. F., 1952. New evidence on the origin of maize. Amer. Nat. 86: 193–202.

29. Randolph, L. F., 1955. History and origin of corn II. Cytogenetic aspects of the origin and evolutionary history of corn. *In* Corn and corn improvement: 16–61. New York, Academic Press.

30. Reeves, R. G., 1944. Chromosome knobs in relation to the origin of maize. Genetics 29: 141–147.

31. ——, 1953. Comparative morphology of the American Maydeae. Texas Agric. Exp. Sta. Bull. 761: 1–26.

32. —— and P. C. Mangelsdorf, 1959. The origin of corn. II. Teosinte, a hybrid of corn and Tripsacum. Bot. Mus. Leafl. Harvard Univ. 18: 357–387.

33. Rogers, J. S., 1950. The inheritance of photoperiodic response and tillering in maize-teosinte hybrids. Genetics 35: 513–540.

34. ——, 1950. The inheritance of inflorescence characters in maize-teosinte hybrids. Genetics 35: 541–558.

35. Singleton, W. R., 1951. Inheritance of corn grass, a macromutation in maize, and its possible significance as an ancestral type. Amer. Nat. 85: 81–86.

36. Stebbins, G. L., Jr., 1950. Variation and evolution in plants. New York, Columbia Univ. Press.

37. Weatherwax, P., 1918. The evolution of maize. Bull. Torrey Bot. Club 45: 309–342.

38. ——, 1919. The ancestry of maize — a reply to criticism. Bull. Torrey Bot. Club 46: 275–278.

39. ——, 1926. Comparative morphology of the oriental Maydeae. Indiana Univ. Studies 73: 3–18.

40. ——, 1950. The history of corn. Sci. Month. 71: 50–60.

41. ——, 1954. Indian corn in old America. New York, Macmillan.

42. ——, 1955. History and origin of corn I. Early history of corn and theories as to its origin. *In* Corn and corn improvement: 1–16. New York, Academic Press.